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Flight activity of carabid beetles on a river margin in relation to fluctuating water levels

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Abstract

Flight should be of great importance for the survival of carabid populations in unstable habitats, such as regularly inundated stream margins. In this study, flight activity of ground beetles was studied by means of window traps at the river banks of the river Elbe in Northern Germany. Flight activity was highest in spring when the water was retreating and after summer floods. A positive correlation was found between flight and air temperature. The predominant flight direction was towards the river, which suggests a recolonisation of the emerging habitats near the edge of receding water. Especially, the very hygrophilous species, such as *Agonum* and *Bembidion* species, seemed to quickly recolonise the free space after inundation. In most species the sex ratio of flying individuals was biased towards females.

Keywords: dispersal, ephemeral habitat, survival, ground beetles, flood.

1. Introduction

The importance of flight in unstable habitats has been shown for different insect taxa, such as crickets (Roff 1994), plant hoppers (Denno et al. 1996), water striders (Harada 1998) and carabid beetles (Den Boer 1970, Den Boer et al. 1980, Aukema 1995). The degree of habitat persistence should be inversely correlated with flight activity. Being characterised by frequent inundations, floodplains constitute very dynamic environments and therefore unstable habitats. This is especially true for river banks that are most directly influenced by the fluctuating waterline during the year. River banks form a transition zone between aquatic and terrestrial habitats that, in part, provide very favourable habitats for carabid beetles (eg. Andersen 1983). However, they are also risky and can quickly change to extremely adverse conditions for carabid survival during floods.

Carabid beetles might adapt to such extreme habitats either by tolerance of submergence during inundation (Palmén 1945, Andersen 1968), vertical migration onto tree trunks (Adis et al. 1997) or by a high dispersal capacity and flight behaviour. The flight potential can be studied by two different approaches: either by investigation of the wing morphs and potential flight abilities within a population or by observation of the actual flight activity. The former was done by Den Boer et al. (1980), Desender (1989), Aukema (1995) and

Bonn et al. (1997) for carabids and often for other insect taxa (Roff 1994 and references within). The latter approach has been applied less frequently, but see Van Huizen (1990) and Matalin (1996).

This study reports on the temporal dynamics of carabid flight activity on river banks using window traps. The traps were installed for three successive years on the river banks of the Elbe to investigate whether flight activity is related to the changing water level of the stream and weather conditions. Furthermore, the flight direction was studied to examine whether a preference in flight direction (either towards or away from the river) could be detected. The sex ratio of the flying ground beetles was also evaluated to see whether sexual differences in flight activity existed.

2. Material and methods

In order to investigate the flight activity of carabid beetles on stream margins, window traps were installed on the river banks of the Elbe over three successive years in 1996 – 98. The river Elbe is characterised by a modified, but basically natural flood regime. Regular inundations of the flood plain occur in winter, spring and summer depending on precipitation in the upstream region. Since dams constrain the water course only in the Czech Republic and downstream of the investigation site, close to Hamburg, the floods occur regularly but not predictably every year.

In 1996 to 1998, four window traps (50 x 60 cm^2 surface area, 115 – 165 cm height, facing East/West, with the river in the East) were placed parallel to the river margin at Pevestorf (53°4'/11°28', N-Germany, stream km 482.5). The river was approximately 300 m wide. The window traps stood close to a *Phalaris* stand in the vicinity of a few old oak trees (site A). A container beneath the windows, filled with 2 % formalin and detergent as preserving agent, collected the flying ground beetles. In order to record flight activity at the water edge, the traps were put as close as possible to the water line. Since they were stationary, the distance to the water varied between 0 – 50 m (see below).

In 1997 and 1998, the traps were modified so that two separate collecting containers were secured under the two sides of the window pane, to allow for a better recording of the flight direction. To test for possible differences in flight activity in different habitats, in 1997, four additional window traps were set up at another site (1.5 km away). These traps were placed at the edge of a nearby Quercus-Ulmus alluvial forest (site B), also parallel to the water line and on the same side of the river (width of river again ca 300 m). In 1998, the flight direction was studied more directly by installing four window traps close to site A (site A*, distance ca 50 m). These traps had a perpendicular orientation (facing North/South), so that flight parallel to the river could also be recorded.

During floods the window traps were reached by the Elbe water and inundated to a height of up to 30 cm. The window traps themselves were not disturbed, however, as the container and the window glass were not reached by the water. Due to the slight slope of the river bank at site A and site A* the water line retreated to a distance of up 30 – 50 m during low water levels in late summer. Here, a large sandy and muddy shore was exposed. At site B, the sand flat was not as extended as at site A and A*, at most 10 – 15 m wide.

In 1996, the traps were checked fortnightly between 22. May and 1. Nov. 1996. In 1997 and 1998, the traps were checked weekly to document the temporal dynamics of the flight activity in more detail (12. March – 5. Nov. 1997; 3. Apr. – 20. Aug. 1998). In late summer to autumn the collecting periods were extended to longer intervals in 1996 and 1997. When a regular check was not possible, the numbers of individuals caught were interpolated to the given interval period.

To relate the flight activity to weather conditions, daily air temperature and wind direction as well as wind velocity were considered. For practical reasons it was not possible to install a data logger for continuous recording at the sites. Therefore, data were taken from the closest meteorological station at Lüchow (ca 25 km away).

3. Results

3.1. Species assemblage

In total 3997 carabid beetles from 103 species were collected with the window traps in the three successive years. A complete taxonomic list is given in App. I. There, the ecological preferences of the species are defined according to literature data (Barndt et al. 1991, Lindroth 1985).

The majority of all ground beetles was hygrophilous (64 % of the species with 91 % of all individuals) and is partly known to exhibit strong habitat preferences. This includes many rare species for this part of Germany (Lower Saxony). Most species are spring breeders, and their overall flight activity was highest in May and June (Fig. 1 a, b and Fig. 2). During this period, mainly *Agonum* and *Bembidion* species were recorded. *Agonum micans* and *Bembidion*

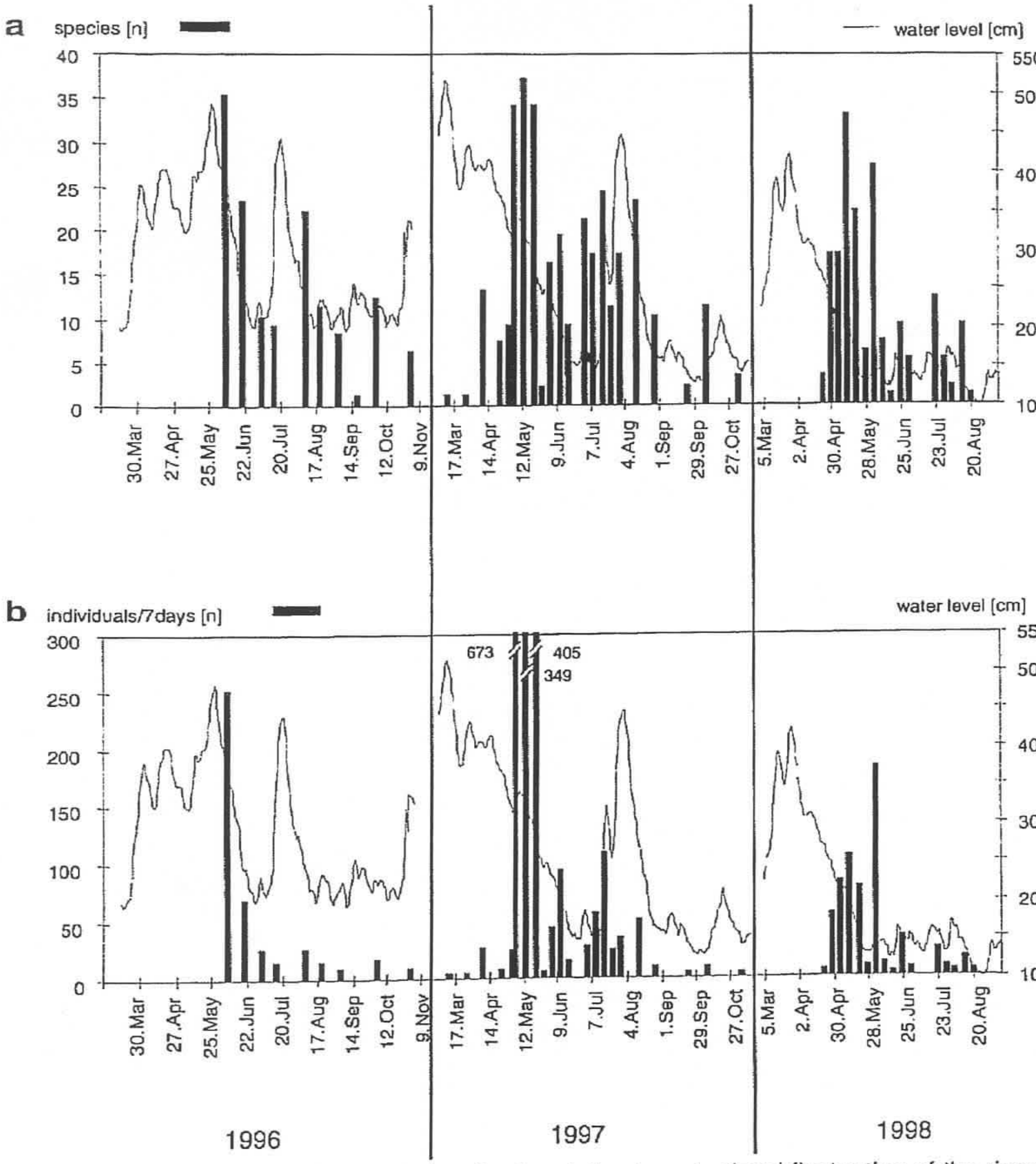

Figure 1. a, b: Flight activity of carabid beetles in relation to water level fluctuation of the river Elbe (recorded at gauge Lenzen). The abundance values are adjusted to a 7 day collecting interval.

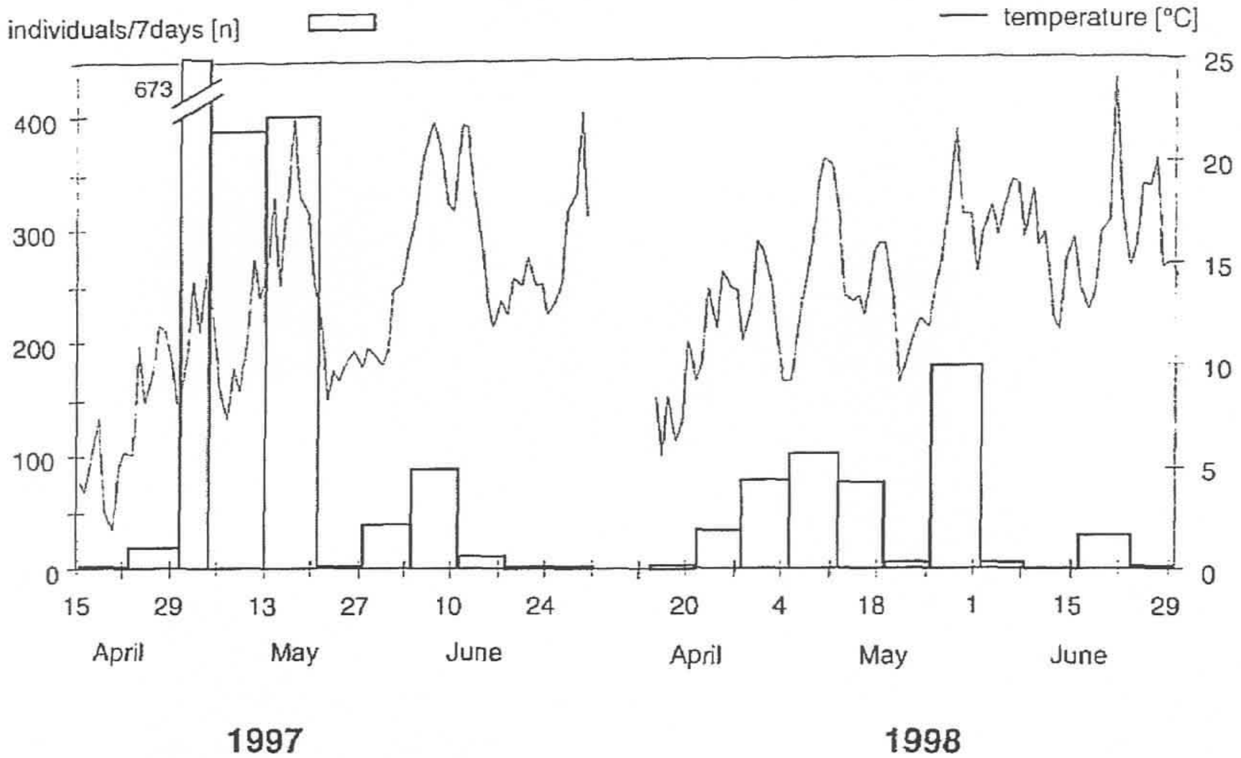

Figure 2. Flight activity of carabid beetles in relation to daily mean air temperature at a height of 2 m. The abundance values are adjusted to a 7 day collecting interval.

biguttatum together with *Stenolophus mixtus* were the most dominant species. These three species made up 51 % of the total catch and were actively flying during the whole survey period (see also Fig. 4 a, b).

App. I also presents the phenology of flight activity per month. Several species, especially many *Bembidion* species demonstrated a continuous flight activity.

Few individuals were recorded flying during autumn. The overall catch rate decreased during the year but the number of species actively flying showed two peaks: one in spring and one in late summer (Fig. 1 a, b). Xerophilous species from the taxa *Amara* and *Harpalus* were caught later in the year, e.g. *Harpalus fröhlichi, Amara bifrons, Amara aulica* and *Pseudoophonus calceatus*. Late flyers also included *Bradycellus harpalinus, Trechus quadristriatus* and the *Calathus* species.

Only 17 % of the recorded species are considered wing dimorphic. All others are constantly macropterous. Within the dimorphic group, only the *Bembidion* species, e.g. *Bembidion guttula*, were abundant in the window traps. Other dimorphic species such as *Pterostichus anthracinus* or *Pterostichus melanarius* were only rarely caught. The latter two species and *Bembidion gilvipes* were, however, frequently collected in pitfall traps on the river bank. Many of these were brachypterous individuals.

3.2. Differences between habitats

In 1997, the catch rates between sites A and B were very different. At the edge of the alluvial forest (site B), less than 20% of the individuals (see Fig. 3b) and 60% of the species recorded at the more open site A were collected. Species missing in the window traps at site B were mostly *Harpalus* and *Amara* spp., but also included eg. *Agonum versutum, Agonum piceum, Bembidion varium, Elaphrus riparius* or *Dyschirius luedersi*, all present on the adjacent silty mud flats close to the water line at site A. At site B only three species not present at site A were caught, including a single teneral specimen of *Platynus assimilis* and six *Dromius quadrimaculatus* caught in late July and August. *Bembidion velox* and *Bembidion femoratum*, two species caught in pitfall traps mainly on sandy soil close to the water, had higher abundances at site B than at site A. Otherwise, the relative species composition did not differ much between the sites.

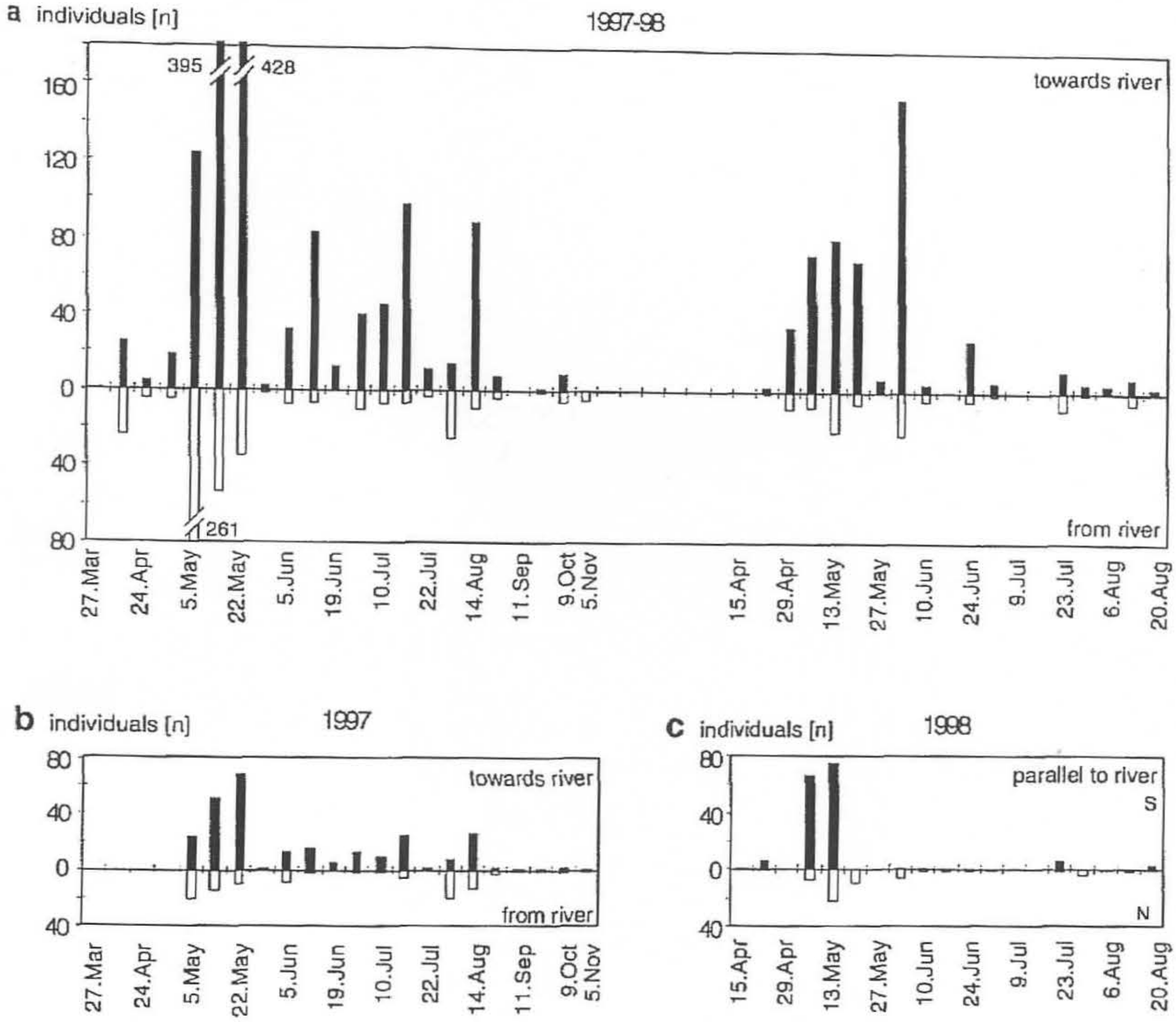

Figure 3. a - c: Flight direction of carabid beetles at three sites in two years. Flight towards and from the stream margin was investigated at sites A(a) and B(b). Window traps at site A* recorded the flight parallel to the river (c) (S - southward N - northward). Absolute numbers of individuals are given for each collecting date (for exact dates see Fig. 1).

3.3. Flight activity in relation to water level fluctuations

The highest flight activities were recorded directly after spring floods (Fig. 1). As the water retreated, the number of actively flying species and individuals increased. In early May 1997, a maximum of 673 flying ind. / week were recorded at site A. In 1996 and 1998, these numbers varied between 102 and 248 ind. / week. The number of species during this period ranged between 27 and 37 in all three years. Note, however, that the collecting intervals differed slightly. An enhanced flight activity could also be observed during summer floods in late July / early August in 1996 and 1997. The number of actively flying individuals was lower than in spring (49 – 106 beetles/week). The maximum species number, 24 species, was comparable, though.

Typical floodplain species like *Agonum dolens*, *Elaphrus riparius* or *Platynus longiventris* were recorded mainly after floods. Some rare species, such as *Amara strenua*, *Agonum lugens*, *Blethisa multipunctata*, *Harpalus luteicornis* or *Pterostichus longicollis* were caught only during this period. Species that are more characteristic for meadows, such as *Poecilus cupreus*, *Pterostichus vernalis* or *Pterostichus nigrita*, also flew during these periods.

3.4. Flight activity and weather

To demonstrate the influence of weather upon flight activity, I graphed the number of carabid beetles captured in the window traps against air temperature (Fig. 2). Two representative periods of high catch rates were chosen. There was enhanced flight activity during periods of high temperatures, for example in early May after the cooler days in April 1997. A similar but smaller flight activity peak was observed in 1998. In both years there was a strong decrease in flight activity at the end of May when daily mean temperatures dropped below 10°C again. Warmer days in June lead again to a somewhat increased flight activity.

There was no apparent relation between flight and the overall wind speed or wind direction during the midday hours (11:00 to 16:00), when most of the window trap catches are reported to occur (see Van Huizen 1979).

3.5. Flight direction

To find out if any directional preference existed in flying carabids, the individuals caught on opposite sides of the window traps were evaluated separately (see Fig. 3 a – c for total activity, and Fig. 4 a – b for two abundant species).

The overall abundance of flying beetles was always higher at site A than at either site A* or site B. More beetles flew towards than away from the river (paired sign test, $p < 0.001$) except on two occasions. Shortly before the flight peaks towards the water on 14. May and 14. Aug. 1997, there was a slightly elevated flight back towards the land, also visible for two common species, *A. micans* and *B. biguttatum* (Fig. 4 a, b).

Considering only species recorded with captures of ten or more specimens, only three species preferentially flew away from the water: *Amara familiaris*, *Agonum piceum* and *Bembidion lunulatum*, during floods on 6. May and 17. June 1997. All other species at all times predominantly flew towards the river.

No change in flight direction was apparent during autumn.

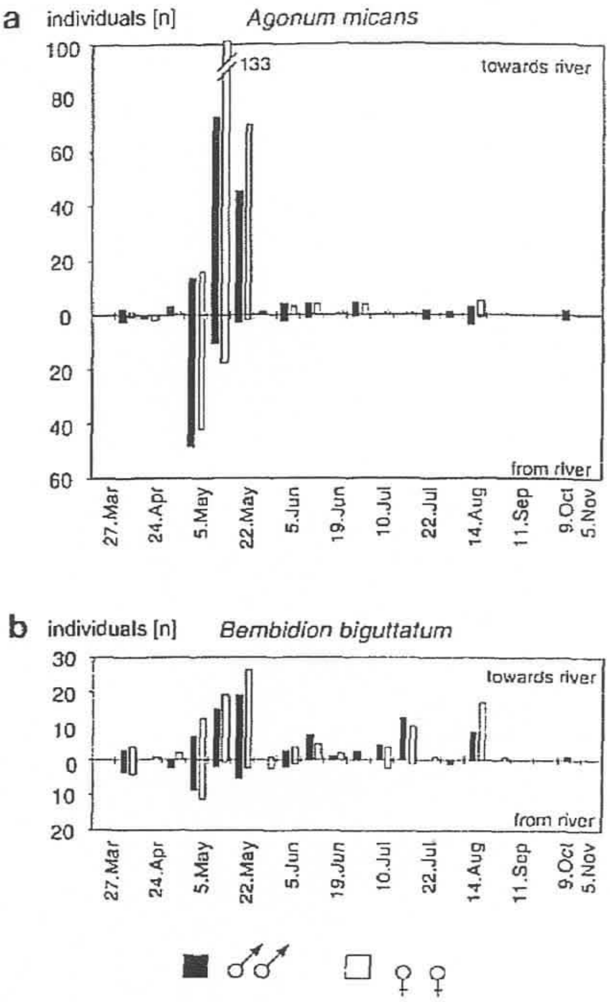

Figure 4. a, b: Sex ratio, seasonal flight activity and flight direction of two selected abundant species, *Agonum micans* and *Bembidion biguttatum*. Absolute numbers of individuals are given for each collecting date (for exact dates see fig. 1).

3.6. Sex ratio

More females than males were captured in the window traps in all three years. Seventeen of the 23 species with catches of >20 individuals had more flying females than males captured (App. I), including the most common species in the taxa *Acupalpus*, *Agonum* and *Bembidion*. More males than females were caught in 5 species only, including *Agonum dolens*, *Amara familiaris* and *Anisodactylus binotatus*. The dominance of females was particularly high in spring. Later in the year, flying males prevailed but on a few occasions only. There was no difference in flight direction preference between the sexes (χ^2 test for all species with n >20 ind., n.s.).

4. Discussion

The highest flight activity occured after or during floods and with the receding water in spring. Mostly adults of predominantly hygrophilous species were caught (Lindroth 1985, Barndt et al. 1991). Many of them were also collected in pitfall traps close to the water line of the river Elbe (Bonn et al. 1997). Some riparian species such as *Bembidion velox* or *Bembidion argenteolum* was no surprise as they are extremely stenotopic and strongly bound to the open sandflats at the waterline (Bonn & Kleinwächter 1999). Mesophilous species from adjacent meadows, such as *Pterostichus melanarius*, *Pterostichus strenuus* or *Poecilus cupreus* were represented by a few individuals only. The same was true for some abundant species of the adjacent alluvial forest at site B, such as *Pterostichus oblongopunctatus* or *Platynus assimilis*. Some of these species exhibit a wing polymorphism, so that their dispersal potential should be lower than that of constantly macropterous species.

A high mobility therefore seems to be of great importance for species living at the fluctuating border between aquatic and terrestrial habitats. Considering the unpredictable flood dynamics, a high disperal capacity should be of great survival value in the risky and unstable environment of floodplains. In a comparative study using pitfall traps and light traps, Matalin (1996) also showed, that especially species from riparian habitats were very active flyers in comparison to species from other habitats. Flight has been shown to be also necessary in other unstable habitats such as polders (Aukema 1995), salt marshes (Desender 1989), agricultural sites (Desender 1986) or for the colonisation of new habitats (Den Boer 1970, Niemelä & Spence 1991).

The time of the highest flight activity also coincided with the reproductive period, since most species captured were spring breeders. Unfortunately, the question whether flight was induced by floods or by reproductive behaviour cannot be studied independently. But if flight was predominantly triggered by reproductive behaviour, flight activity should vary little between successive years. In 1998, a year with unusually low water levels and only little inundation, however, flight activity was lowesk. This supports the hypothesis that enhanced flight occurs as a direct reaction to floods.

Flight activity is strongly influenced by weather conditions, as also shown by Van Huizen (1979). In this study, there seems to be a response to high average daily temperatures. I suggest that especially peak temperatures during the day are relevant. Wind may also be of importance, but no correlation between the overall wind velocity nor direction recorded at the closest meteorological station (25 km away) could be found. As wind changes quickly and has probably high local deviations, continuous measurements at the site and shorter collecting intervals might more precisely indicate a possible correlation. But again, the difference of flight activity between the years cannot be explained by weather conditions, since these were comparable.

So, flight activity seems a reaction to the retreat of the floods. This probably enables carabid beetles to reach virgin habitats in the immediate vicinity of the water edge and to quickly recolonise the shoreline. After inundations these habitats should offer abundant food resources, mainly collembola and diptera (Zulka 1994) or aquatic invertebrates (Hering & Plachter 1997). The dominant flight direction of most carabid beetles towards the water (see Fig. 3 and 4) throughout the whole year is in accordance with this assumption. Only shortly before flood peaks is the main flight direction turned towards the land. This could be interpreted as an escape reaction. Olfactory stimuli, such as volatiles from blue green algae (Evans 1984) or prey (Kielty et al. 1996) could guide the flying carabids towards the freshly emerged sandy beaches or silty mud flats.

The comparison of the two crosswise placed sets of window traps shows that flight was most often directed towards the river margin, but beetles also flew parallel to the water line in May. Then, the water level was so high that the water edge was close to the window traps. Under those conditions, the traps might not only record

,migratory' but also ,general' flight without any particular direction. Whereas most ground beetle species are reluctant to fly, species living at the direct water edge, such as *Bembidion velox*, fly readily. Kaufmann (1986) reports this for a North American *Bembidion* species, as well. I observed *Bembidion quadripustulatum*, *B. dentellum* and *B. semipunctatum* and *Agonum marginatum* to settle on artificial styroform ,islands' fastened in the water, about 4 – 10 m from the shoreline (Bonn, unpubl. data). This supports the hypothesis that flight is of high importance within these temporally and spatially unstable habitats.

A migratory flight back towards hibernation habitats during autumn could not be recorded (but see Van Huizen 1977). Maybe, flight towards hibernation sites is much more random and not as clearly directed as the flight towards the water line after floods. Instead, walking may be involved (Lang & Pütz 1999).

Carabids may move towards the freshly exposed alluvial flats not only in search of abundant food. These areas at the water edge may also offer suitable substrates for oviposition (Adis et al. 1997), since the high soil moisture in the immediate vicinity of the waterline should prevent dessication of the sensitive egg and larval stages. Indeed, more females than males were caught, especially during spring (see Fig. 4a). It is possible that females actively colonise the free space at the waterline for oviposition. Some carabids are even able to oviposit in still inundated sites due to the possibility of submers development of eggs (Andersen 1968). The short development time of such species (Kaufmann 1986, Adis et al. 1997) can also be considered an adaptation to such conditions. It has, however, often been suggested that a trade off between investment in flight capability and reproduction should exist (eg. Den Boer et al. 1980, Roff 1994, Zera & Denno 1997). The oogenesis flight syndrom assumes that the presence of developed or developing oocytes is somehow inhibitory to migratory behaviour (Johnson 1969). However, window trap studies over 12 years by Van Huizen (1990) found many females that flew with their ovaries partly filled with eggs. This was especially true for species from temporary habitats. Aukema (1991) even reported that long winged females in a wing dimorphic species had a higher fecundity than short winged females. This is a strong indication that flight may be vital for (re)establishing populations in new habitats.

In the Amazonian inundation forest Adis et al. (1997) could show that young tenerals of *Colliuris batesi* escape floods by flight to adjacent dryland forests and return after the inundation period as sexually mature individuals to recolonise the drying forest floor and lay eggs close to the receding water edge. Within this wing dimorphic species macropterous morphs occur only prior and during times of floods (Adis et al. 1997). In my study, wing dimorphic species, such as *Pterostichus gracilis*, *P. anthracinus*, *P. vernalis* or *Clivina fossor*, were also mainly caught after floods in the window traps. As mentioned already, however, flight seems to be most important within constantly macropterous species that live in the direct vicinity of the water edge. Especially after long inundation periods Zulka (1994) and Wohlgemuth - von Reiche (pers. comm.) both recorded great numbers of typical floodplain species, such as *Agonum dolens*, *Blethisa multipunctata* or *Platynus longiventris* in the new generation. These species may successfully utilise the short term optimal abiotic (eg. soil moisture) and biotic (abundance of food, absence or low density of competitors and predators) conditions on the river banks and may thus compensate for losses during unpredictable floods.

To summarise the results of this study, it can be assumed that flight is an important trait for the survival of carabid beetles on river banks. Enhanced flight activity during and after floods may not only allow to escape adverse conditions but rather help to quickly invade the free space when the water recedes and to exploit the ephemeral but plentiful food supply on the river banks. A fast recolonisation by flight may therefore ensure the persistence of carabid populations in these temporally and spatially unstable habitats.

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References

Adis, J., M. A. Amorim, T. L. Erwin & T. Bauer 1997: On ecology, life history and survival strategies of a wing-dimorphic ground beetle (Col.: Carabidae: Odacanthini: Colliuris) inhabiting Central Amazonian inundation forests. — Studies on Neotropical Fauna and Environment 32: 174-192.

Andersen, J. 1968: The effect of inundation and choice of hibernation sites of Coleoptera living on river banks. — Norsk Entomologisk Tidsskrift 15: 115-133.

Andersen, J. 1983: The habitat distribution of species of the tribe Bembidiini (Coleoptera, Carabidae) on banks and shores in Northern Norway. — Notulae Entomologicae 63: 131-142.

Aukema, B. 1991: Fecundity in relation to wing-morph of three closely related species of the melanocephalus group of the genus Calathus (Coleoptera: Carabidae). — Oecologia 87: 118-126.

Aukema, B. 1995: The evolutionary significance of wing dimorphism in carabid beetles (Coleoptera: Carabidae). — Researches in Population Ecology 37: 105-110.

Barndt, D., S. Brase, M. Glauche, B. Kegel, R. Platen & H. Winkelmann 1991: Die Laufkäferfauna von Berlin (West) - mit Kennzeichnung und Auswertung der verschollenen und gefährdeten Arten (Rote Liste 3. Fassung). — Landschaftsentwicklung und Umweltforschung 56: 243-275.

Bonn, A., K. Hagen & B. Helling 1997: Einfluß des Überschwemmungsregimes auf die Laufkäfer- und Spinnengemeinschaften in Uferbereichen der Mittleren Elbe und Weser. — Arbeitsberichte Landschaftsökologie Münster 18: 177-191.

Bonn, A & M Kleinwächter (1999): Microhabitat distribution of spider and ground beetle assemblages (Araneae, Carabidae) on frequently inundated river banks of the River Elbe. — Zeitschrift für Ökologie und Naturschutz 8: 109-123.

Den Boer, D. J., T. H. P. Van Huizen, W. Den Boer-Daanje, B. Aukema & C. F. M. Den Biemann 1980: Wing polymorphism and dimorphism in ground beetles as stages in an evolutionary process (Coleoptera: Carabidae). — Entomologia Generalis 6: 107-134.

Den Boer, P. J. 1970: On the significance of dispersal power for populations of carabid-beetles (Coleoptera, Carabidae). — Oecologica 4: 1-28.

Denno, R. F., G. K. Roderick, M. A. Peterson, A. F. Huberty, H. G. Döbel, M. D. Eubanks, J. E. Losey & G. A. Langellotto 1996: Habitat persistence underlies intraspecific variation in the dispersal strategies of planthoppers. — Ecological Monographs 66: 389-408.

Desender, K. 1986: On the relation between abundance and flight activity in carabid beetles from a heavily grazed pasture. — Journal of Applied Entomology 102: 225-231.

Desender, K. 1989: Heritability of wing development and body size in a carabid beetle, *Pogonus chalceus* MARSHAM, and its evolutionary significance. — Oecologia 78: 513-520.

Evans, W. G. 1984: Odor-mediated responses of *Bembidion obtusidens* (Coleoptera: Carabidae) in a wind tunnel. — Canadian Entomologist 116: 1653-1658.

Harada, T. 1998: To fly or not to fly: response of water striders to drying out of habitat. — Ecological Entomology 23: 370-376.

Hering, D. & D. Plachter 1997: Riparian ground beetles (Coleoptera, Carabidae) preying on aquatic invertebrates: a feeding strategy in alpine floodplains. — Oecologia 111: 261-270.

Johnson, C. G. 1969: Migration and dispersal of insect by flight. — Methuen, London.

Kaufmann, T. 1986: Bionomics of *Bembidion confusum* (Coleoptera: Carabidae) with special reference to its reproductive adaptations to the stream-margin habitat. — Annals of the Entomological Society of America 79: 975-984.

Kielty, J. P., L. J. Allen-Williams, N. Underwood & E. A. Eastwood 1996: Behavioral responses of three species of ground beetle (Coleoptera: Carabidae) to olfactory cues associated with prey and habitat. — Journal of Insect Behavior 9: 237-250.

Lang, O. & S. Pütz 1999: Frühjahrsbesiedlung eines im Winter überfluteten Naßpolders durch Spinnen und Laufkäfer im Nationalpark Unteres Odertal. — Limnologie aktuell 9: 171-195.

Lindroth, C. H. 1985: The Carabidae (Coleoptera) of Fennoscandia and Denmark. vol 1-2. — Fauna Entomologica Scandinavica 15: 1-447.

Matalin, A. V. 1996: Use of light traps in ecological studies of ground beetles (Coleoptera, Carabidae). — Entomological Review 76: 282-293.

Niemelä, J. & J. R. Spence 1991: Distribution and abundance of an exotic ground-beetle (Carabidae): a test of community impact. — Oikos 62: 351-359.

Palmén, E. 1945: Über Quartierwechsel und submerse Überwinterung einiger terrestrischer Uferkäfer. — Annales Entomoligici Fennici 11: 22-34.

Roff, D. A. 1994: Habitat persistence and the evolution of wing dimorphism in insects. — The American Naturalist 144: 772-798.

Trautner, J., G. Müller-Motzfeld & M. Bräunicke 1997: Rote Liste der Sandlaufkäfer und Laufkäfer Deutschlands (Coleoptera: Cicindelidae et Carabidae). 2. Fassung, Stand Dezember 1996. — Naturschutz und Landschaftsplanung 29: 261-273.

Van Huizen, T. H. P. 1977: The significance of flight activity in the life cycle of *Amara plebeja* Gyll. (Coleoptera, Carabidae). — Oecologia 29: 27-41.

Van Huizen, T. H. P. 1979: Individual and environmental factors determining flight in carabid beetles. — Miscellaneous Papers Landbouwhogeschool (Wageningen) 18: 199-211.

Van Huizen, T. H. P. 1990: ‚Gone with the wind': Flight activity of carabid beetles in relation to wind direction and to the reproductive state of females in flight. — In: N. E. Stork (ed.), The role of ground beetles in ecological and environmental studies: 269-275. Athenaeum Press, Newcastle upon Tyne.

Zera, A. J. & R. F. Denno 1997: Physiology and ecology of dispersal polymorphism in insects. — Annual Review of Entomology 42: 207-30.

Zulka, K. P. 1994: Carabids in a Central European floodplain: species distribution and survival during inundations. — In: K. Desender, M. Dufrene, M. Loreau, M. L. Luff & J. P. Maelfait (eds.), Carabid Beetles: Ecology and Evolution: 399-405. Kluwer Academic Publisher.

Appendix I. Taxonomic list of all species recorded in window traps during 1996 - 1998 (nomenclature after Trautner et al. 1997). The ecological preference and the hibernation mode are taken from literature data (Barndt 1991, Lindroth 1985), the wing morph phenotype is taken from own investigations from pitfall trap catches (Bonn et al. 1997) (h/(h) - (predominantly) hygrophilous, eu - euryoecious, x/(x) - (predominantly) xerophilous, w/(w) (predominantly) forest species, arb - arboricolous, hal - halophilous, rip - riparian; l/(l) - (predominantly) imago hibernation, L/(L) - (predominantly) larvae hibernation; ma - macropterous, di - wing dimorphic).
The seasonal flight activity is indicated by stars, given as the accumulated sum per month over three years (* 1 - 10 ind., ** 11 - 50 ind., *** > 50 ind.). The sex ratio is given as the proportion of females of the total catch rate. Sex was not identified within the genera *Clivina* and *Dyschirius*.

Species	Habitat affinity	Hibernation mode	Wing type	Flight activity/ month								%, females	total caught, 1996-98
				March	April	May	June	July	August	September	October		
Acupalpus dubius	h	l	ma			**	*	**	*	*		100	13
Acupalpus exiguus	h	l	ma		*	***	***	**	**	*		58	384
Acupalpus flavicollis	h	l	ma			*	*					67	3
Acupalpus meridianus	(x)	l	ma			*	*					56	9
Acupalpus parvulus	h	l	ma		*	**	**	**	*			58	55
Agonum afrum	h (w)	l	di		*	**	**	*	*			61	73
Agonum dolens	h	l	ma			**	**		*			40	53
Agonum fuliginosum	h	(l)	di			*	*					50	4
Agonum gracile	w	l	ma			*	*					0	2
Agonum lugens	h (w)	(l)	ma				*					100	1
Agonum marginatum	h	l	ma			*	*	*		*		58	12
Agonum micans	h	l	ma		**	***	***	*	**	*	**	54	946
Agonum muelleri	(h)	l	ma		*		*			*		100	4
Agonum pelidnum	h	(l)	ma			*	*					100	2
Agonum piceum	h	l	ma		*	**	*		*			51	41
Agonum sexpunctatum	(h)	l	ma				*					100	1
Agonum versutum	h	l	ma		*	**	**	*	*			58	66
Agonum viduum	h	l	ma			*	*					100	4
Agonum viridicupreum	h	l	ma			*						0	1
Amara aenea	(x)	l	ma		*	*						50	4
Amara apricaria	(x)	L	ma					*	*			60	5
Amara aulica	(x)	L	ma					*				50	2
Amara bifrons	x	L	ma				*	**	*			61	18
Amara communis	(h)	(l)	ma		*	*						57	7
Amara familiaris	(x)(w)	l	ma		*	**	*	*	*		*	43	49
Amara fulva	(x)	(l)	ma						*			0	1
Amara lunicollis	(x)(w)	l	ma			*						50	2
Amara majuscula	?h	(l)	ma				*	*	*			50	12

Species	Habitat affinity	Hibernation mode	Wing type	Flight activity/ month March	April	May	June	July	August	September	October	%, females	total caught, 1996-98
Amara ovata	(h)(w)	(l)	ma			*						40	5
Amara plebeja	eu	l	ma			**	*	*			*	50	18
Amara similata	eu	*l*	ma			**	*	*				84	25
Amara strenua	h	(l)	ma				*		*			17	6
Amara tibialis	x	l	ma			*						100	1
Anchomenus dorsalis	(x)	l	ma						*			100	1
Anisodactylus binotatus	(h) w	l	ma		*	***	**	*		*		44	108
Anthracus consputus	h	l	ma		*	***	**	*	*			66	195
Asaphidion flavipes agg.	eu	l	ma			*						100	1
Badister bullatus	(x)(w)	l	ma		*	*						83	6
Badister collaris	h	l	ma			*	*	*				75	8
Badister dilatatus	h	l	ma		*	**	*	*	*			57	30
Badister lacertosus	(h) w	l	ma			*			*			60	5
Badister meridionalis	h	l	ma			*		*	*			60	5
Badister sodalis	h	l	ma			*						100	1
Badister unipustulatus	h (w)	l	ma		*	**	*	*	*			47	17
Bembidion argenteolum	h, rip	l	ma				*			*		50	4
Bembidion articulatum	h	*l*	ma			*						0	1
Bembidion assimile	h	l	di		*	*	*	*	*			47	19
Bembidion biguttatum	h	l	ma		**	***	***	**	**	*	*	55	518
Bembidion dentellum	h	l	ma		*	**	**	*	*		*	51	55
Bembidion doris	h	l	ma			*						100	1
Bembidion femoratum	eu	(l)	ma		*	**	*	**	**		*	66	91
Bembidion fumigatum	h,hal,rip	(l)	ma			*	*	*	*		*	45	11
Bembidion gilvipes	h (w)	l	di			*						0	2
Bembidion guttula	h	l	di	*	**	**	**	**	**	*	*	60	112
Bembidion lunulatum	h	l	ma			*		**				36	22
Bembidion octomaculatum	h	l	ma			*	*	*	**	*		49	36
Bembidion properans	(x)	(l)	di				*					100	1
Bembidion quadrimaculatum	(x)	(l)	ma		*	*		*	*			61	18
Bembidion semipunctatum	h	l	ma		*	**	**	*	*		*	59	58
Bembidion varium	h	l	ma			*	*	*	*	*	*	64	14
Bembidion velox	h, rip	l	ma				*	*	*			82	11
Blethisa multipunctata	h	l	ma			*	*					100	2
Bradycellus harpalinus	eu	(l)	di						*		*	100	4
Calathus cinctus	x	(L)	di						*			0	1

Species	Habitat affinity	Hibernation mode	Wing type	Flight activity/ month								%, females	total caught, 1996-98
				March	April	May	June	July	August	September	October		
Calathus melanocephalus	(x)	(L)	di					*				0	1
Chlaenius nigricornis	h	l	ma			*	*					83	6
Clivina fossor	eu	l	di		*	**	*		*			-	38
Demetrias atricapillus	(h)	l	ma			*						100	2
Dromius quadrimaculatus	w, arb	l	ma					*	*			43	7
Dyschirius aeneus	h	l	ma			*		*				-	4
Dyschirius luedersi	h	l	ma			*		*	*	*		-	14
Elaphrus cupreus	h (w)	l	ma			*						50	2
Elaphrus riparius	h, rip	l	ma			*	*	*				88	8
Harpalus distinguendus	(x)	(l)	ma			*						100	1
Harpalus froehlichii	x	l	ma						*	*		29	7
Harpalus latus	(h)(w)	l	ma				*		*			100	2
Harpalus luteicornis	(x)	l	ma			*	*					80	5
Harpalus rubripes	x	(l)	ma				*					100	1
Harpalus rufipalpis	x	(l)	ma				*					75	4
Harpalus smaragdinus	(x)	(L)	ma				*					0	1
Loricera pilicornis	(h)(w)	(l)	ma		*	*	*			*		45	11
Ophonus puncticeps	(x)	(L)	ma						*			0	1
Notiophilus biguttatus	w	(l)	di			*	*					50	2
Oodes helopioides	h	l	ma				*					0	1
Ophonus rufibarbis	(x)(w)	(l)	ma				*	*				0	3
Ophonus signaticornis	(x)	l	ma			*	*					67	3
Panageus cruxmajor	h	l	ma			*						100	2
Platynus assimilis	h (w)	l	ma				*	*				50	2
Platynus longiventris	h (w)	l	ma			**	*	*	*		*	64	25
Poecilus cupreus	(h)	l	ma			*	*	*	*		*	57	14
Pseudoophonus calceatus	x	l	ma						*			50	2
Pseudoophonus rufipes	(x)	(l)	ma				*	*	*			44	9
Pterostichus anthracinus	h (w)	l	di			*				*		67	3
Pterostichus gracilis	h	(l)	ma			*					*	56	9
Pterostichus longicollis	h	(l)	di			*	*					100	2
Pterostichus melanarius	eu	l	di				*		*			50	2
Pterostichus nigrita cf.	h (w)	(l)	ma		*		*			*		43	7
Pterostichus vernalis	h	l	di			*						50	6
Stenolophus mixtus	h	l	ma		*	***	***	**	**	*	*	85	556
Stenolophus skrimshiranus	h	l	ma			*						57	7

Species	Habitat affinity	Hibernation mode	Wing type	Flight activity/ month								%, females	total caught, 1996-98
				March	April	May	June	July	August	September	October		
Stenolophus teutonus	h	I	ma			*	*					67	3
Trechus quadristriatus	(x)	(I)	ma					*	**	*	*	59	27
Trichocellus placidus	h w	I	ma			*			*	*		50	10
Number of individuals				3	133	2127	992	344	293	53	52		3997
Number of species				1	26	72	64	44	47	19	16		103